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Butterfly (Insecta: Lepidoptera) assemblage structure along an upland-highland elevational gradient in a Brazilian tepui

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ABSTRACT

Pantepui is a biogeographic province in the Guiana Highlands, considered an archipelago of tabletop mountains (*tepuis*) with a unique and poorly-known biota. Here, we investigate the butterfly assemblage structure along an elevational gradient on the Brazilian side of the Uei Tepui. We sampled butterflies in 14 plots, each at least 500 m apart, ranging from 1000 to 1820 m elevation. Each plot contained four baited traps in the canopy and four in the understory, set in pairs. We also performed standardized active sampling using an entomological net in each plot and additionally sampled butterflies opportunistically between 920 and 2100 m to complement the butterfly inventory. Over 21 days, we sampled 299 individuals from 93 species of butterflies. In the sampling plots, richness and abundance decrease considerably with altitude, and most species have been recorded (74%) in the Amazonia lowlands. However, there was a marked change in species richness, abundance, and composition at 1330 m compared to lower altitudinal plots. From this altitude, the species replacement (turnover) decreased, while the occurrence of endemic species strongly increased, especially in elevations above 1500 m. Our results highlight elevational effects such as spatial limitation and filtering on butterfly diversity, reinforcing the importance of conservation in this megadiverse region.

KEYWORDS: Amazonia, altitudinal gradient, beta-diversity, community, endemism.

Estrutura da assembleia de borboletas (Insecta: Lepidoptera) ao longo de um gradiente altitudinal de terras altas em um tepui brasileiro

RESUMO

Pantepui é uma província biogeográfica nas terras altas do Escudo das Guianas, considerada um arquipélago de montanhas em forma de mesa (*tepuis*) com uma biota única e pouco conhecida. Aqui, investigamos a estrutura da assembleia de borboletas ao longo de um gradiente altitudinal no lado brasileiro do Uei Tepui. Amostramos borboletas em 14 parcelas, cada uma com pelo menos 500 m de distância, variando de 1000 a 1820 m de altitude. Cada parcela continha quatro armadilhas atrativas no dossel e quatro no sub-bosque, configuradas em pares. O esforço de coleta foi complementado por busca ativa padronizada usando rede entomológica e também de forma oportunista entre 920 e 2100 m para complementar o inventário de borboletas. Ao longo de 21 dias, amostramos 299 indivíduos de 93 espécies de borboletas. Nas parcelas, a riqueza e a abundância diminuíram consideravelmente com a altitude, e a maioria das espécies foi registrada (74%) nas terras baixas da Amazônia. No entanto, houve uma mudança marcante na riqueza de espécies, abundância e composição aos 1330 m em comparação com as parcelas altitudinais mais baixas. A partir desta altitude, a substituição de espécies (*turnover*) diminuiu, enquanto a ocorrência de espécies endêmicas aumentou fortemente, especialmente em elevações acima de 1500 m. Nossos resultados destacam os efeitos da elevação, como limitação espacial e o filtro ambiental, sobre a diversidade de borboletas, reforçando a importância da conservação nesta região megadiversa.

PALAVRAS-CHAVE: Amazônia, beta-diversidade, comunidade, endemismo, gradiente altitudinal

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INTRODUCTION

Biodiversity patterns along altitudinal gradients have been crucial to understanding species distribution in space and time (Rahbek et al. 2019). From an evolutionary perspective, there is a consensus that mountains greatly influence species diversification and endemism (Antonelli et al. 2018; Quintero and Jetz 2018; Perrigo et al. 2020). Mountains provide marked climatic variations in short spatial distances, and these differences result in large changes in the local geophysical and environmental conditions, which influence the occurrence and persistence of species (Körner 2007).

The Pantepui is a biogeographic province of the Guiana Highlands composed of a set of high mountains (1500-3000 m in elevation) surrounded by Amazonian lowland rainforests and savannas, considered an archipelago of sky islands (Mayr and Phelps 1967; Berry and Riina 2005). It is one of the oldest geological formations in South America (Rull et al. 2019a), characterized by typical flat-topped mountains, locally known as *tepuis*. The *tepuis* are remnants of a long-standing erosional process accumulated since the Precambrian times (Briceño and Schubert 1990). The upper portions (hereafter highlands – above 1500 m) display highly differentiated ecosystems regarding geological, geomorphological, geochemical, and biological aspects. These sharp differences along altitudinal zonation in *tepuis* are usually not found in other mountains where continuous formation has no significant interruption and present a more gradual elevational change (Viloria and Costa 2019). Due to these unique features related to geomorphological formations, biotic composition, and endemism, Pantepui is considered one of the areas of endemism in the Neotropics (Morrone 2017).

The elevational stages of Pantepui mountains are classified based on the phytogeographic criteria, with lowlands (0-500 m a.s.l. - above sea level), uplands (500-1500 m a.s.l.), and highlands (above 1500 m a.s.l.) representing the general distribution and diversity patterns of Pantepuian organisms (for more details, see Huber 1995 and Rull et al. 2019a). Although such elevational stages based on the phytogeographic criteria have been formalized, the actual categorization of the highlands can vary between 1200-1500 m depending on the *tepui* environment and biotic criteria (Huber 1987; Rull et al. 2019a). The highlands are the elevational stage where endemic species are usually found and despite the high vegetational endemism (~ 41%; Riina et al. 2019), species richness, abundance, and diversity of plants and animals tend to be lower compared to the uplands and lowlands (Berry and Riina 2005; Lew and Lim 2019; Ochoa and Rojas-Runjaic 2019; Nogueira et al. 2021).

Organisms with a strong association with plants usually respond similarly to changes in vegetation composition and structure (Dennis et al. 2004; Oliveira et al. 2021). For instance, most butterfly species are host-plant specialists (DeVries 1986), and their community similarity tends to decrease with more heterogeneous and diverse plant communities (Steffan-Dewenter and Tscharntke 2000; Kumar et al. 2009). Studies of butterflies along an elevational gradient in two mountain chains in Brazil (e.g., Serra do Mar and Espinhaço) showed a strong correlation between butterfly and plant composition and diversity (Carneiro et al. 2014; Beirão et al. 2020; Pires et al. 2020). Therefore, the phytogeographic definition can be used as a surrogate to investigate the diversity patterns of other organisms (Viloria and Costa 2019).

Understanding the variation of butterfly species composition along elevational gradients (spatial β-diversity) may provide valuable insights into how the community of this important group of bioindicators (Bonebrake et al. 2010) is structured in unique regions like the Pantepui. For instance, β-diversity partitioning into turnover and nestedness components can shed light on the underlying processes shaping community structure (Baselga 2010). Spatial β-diversity can be decomposed into turnover, which reflects species replacement between sites and is usually associated with environmental and biotic heterogeneity (Socolar et al. 2016), and nestedness, which represents an ordered species loss across sites, where sites with fewer species are subsets of richer ones (Baselga 2010; Legendre 2014).

The present study aimed to elucidate the structure of the butterfly community in Uei Tepui and evaluate the diversity and endemism patterns along the elevational gradient. We hypothesized that (1) butterflies' richness, abundance, and diversity should decrease with elevation, and the main compositional change, including the appearance of endemic species, should occur between 1200 and 1500 m a.s.l., as reported for different taxa in Pantepui. (2) We also expect that turnover will be more dominant than nestedness, and the upland butterfly community will present higher species turnover than the highland community because of more space and resource availability on lower elevations.

MATERIAL AND METHODS

Study area

This study was carried out in the eastern portion of the Pantepui formation (Figure 1a, b). Sampling was undertaken at the Uei Tepui (5°5'N; 60°35'W) in the northern part of the Brazilian Amazon in the Roraima State (Figure 1c). Uei Tepui is located on the Brazilian and Venezuelan borders. It has a maximum elevation of 2150 m, with a summit area of 2.5 km^2 and a sloped area of 20 km^2 (Rull et al. 2019a). On the Brazilian side, the Uei Tepui is covered by two overlapping protected areas, the Raposa Serra do Sol Indigenous Land (Fundação Nacional dos Povos Indígenas – FUNAI) and the Mount Roraima National Park (Instituto Chico Mendes de Conservação da Biodiversidade – ICMBio; Figure 1d). The vegetation zonation along elevation can be seen in Figure 1, where Figures 1e-g depict the upland and Figure 1h-j the highland.

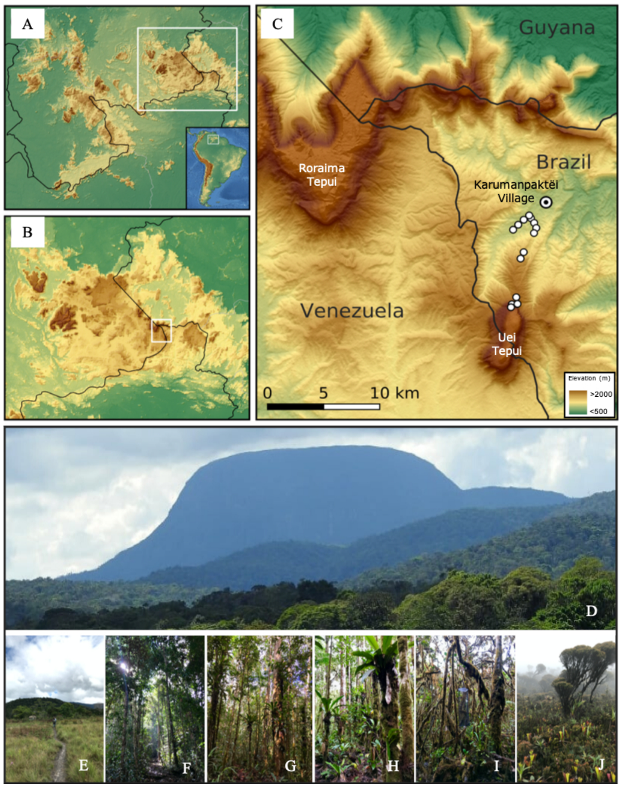

Figure 1. (A) Pantepui map in the northernmost part of South America with **(B)** the Eastern Pantepui region and **(C)** the study region showing the location of each sampling unit (plot) in Uei Tepui, Roraima State, Brazil. **(D)** Uei Tepui view and its flat-top summit with continuous upland-highland forests (photo: Ramiro Melinski); **(E)** Open area at 920 m a.s.l.; **(F)** Forest structure at 1000-1100 m a.s.l.; **(G)** Forest at 1300 m a.s.l.; **(H)** Epiphytes and mosses on trunks at 1500 m a.s.l.; **(I)** Butterfly trap at 1820 m a.s.l.; **(J)** Uei Tepui summit at 2100 m a.s.l.

The phytogeographical characterization of the elevational stages of the Uei Tepui aligns with the general characterization of *tepuis* (personal observation). The surrounding lowlands of the Uei Tepui are usually covered by open savannas with small herbaceous formations or by tropical wet forests (Rull et al. 2019a). The uplands include open savannas, lower montane and montane vegetation, with mixed forest formations also present (Rull et al. 2019a). In the highlands, evergreen cloud forests are found on the slopes. As the elevation increases, there is a decrease in the canopy height towards the summit, where shrubs, carnivorous plants, grasses, and open-rock communities often dominate (Rull et al. 2019a).

Sampling design and data collection

Butterflies were collected at the end of the wet season, from November 29th to December 19th of 2019, in 14 200-m long sampling plots (eight in the uplands, and six in the highlands) along a steep forest slope ranging from 1000 to 1820 m a.s.l. (~15 km). Most plots were at least 500 m apart from each other, except for the higher altitudinal plots (1820 m a.s.l.), which were separated by 200 m due to spatial limitations and logistical constraints.

In each plot, we placed four pairs of Van Someren-Rydon type traps (Rydon 1964) 50 m apart, each pair consisting of one trap in the understory (~ 1– 1.5 m high) and one in the canopy (~ 15– 20 m high). The higher altitudinal plots had only understory traps due to the low canopy height (~5 m; Figure 1i). Traps contained bait made of bananas and sugarcane juice fermented for 48 hours and were kept open for seven consecutive days, being checked every 48 hours (Freitas et al. 2014), resulting in a total sampling effort of 728 trap-days (56 trap-days per plot, except for the two plots at 1820 m a.s.l. which had half the trapping effort: 28 trap-days). We followed the butterfly sampling protocol of the Brazilian Biodiversity Monitoring Program (*Programa Nacional de Monitoramento da Biodiversidade do Instituto Chico Mendes – Programa Monitora*; Brasil 2022), using a bait proportion of 3 kg of bananas to 1 liter of sugarcane (Nobre et al. 2014). We choose to check the traps every 48 hours to be able to sample in a larger number of plots. Thus, every day, we checked different plots distant from each other. Standardized active searches using entomological nets were performed along all plots, enabling comparable analysis across sites. This sampling was conducted simultaneously with trap checks, with two collectors walking at 1 km h^{-1} and collecting all butterflies sighted up to 2.5 m on each side of the transect. This method allowed us to sample both fruit-feeding and nectar-feeding butterflies.

Since this was the first biological expedition in this region, we took advantage of the opportunity to document as many butterfly species as possible. Therefore, in addition to standardized sampling, we conducted opportunistic surveys (e.g., non-standardized method) outside sampling units, including campsite areas and the Ingarikó people's village, across an elevational range of 920 to 2100 m a.s.l. using entomological nets. We also surveyed the summit of Uei Tepui, but we did not detect any butterflies, likely due to the continuous rainy conditions. Butterflies sampled during these opportunistic surveys were not included in the statistical analysis, as mentioned below.

Butterflies were identified at the species and subspecies levels using an online guide (www.butterfliesofamerica.com), including a book chapter and taxonomic literature about Pantepui butterflies (Costa et al. 2017; Viloria and Costa 2019; Costa et al. 2020). Expert taxonomists in Neotropical and Pantepui butterfly fauna, Mauro Costa, Ángel Viloria, Andrew Nield, and Patrick Blandin, verified the butterfly identifications. Specimens were collected under permissions SISBIO 72093-1 and 57444. All collected butterflies were deposited in the Entomological Collection of the National Institute of Amazonian Research (INPA), and some individuals of the most abundant species were also deposited in the Community Ecology Lab of the Federal University of Amazonas (UFAM).

We compiled butterfly studies in the lowlands of the Brazilian Amazon with an available species list to better characterize the uniqueness of the butterfly fauna of Uei Tepui. The second author, Mauro Costa, classified the endemic species, and we also consulted the literature on Pantepui butterflies (Costa et al. 2017; Viloria and Costa 2019; Costa et al. 2020).

Statistical analysis

In this study, all analyses were performed using data from sampling units (plots from 1000 to 1820 m a.s.l.) where standardized methods were employed. For each plot, we combined butterflies sampled in the traps of both strata and those captured with the entomological net from the transect walk. To account for minor altitudinal variation among traps, we placed them at similar elevations whenever possible. To control any larger variation, we used the mean altitude of the four pairs of traps installed along each sampling plot to represent its elevation (Supplementary Material, Table S1).

To determine if our rapid inventory provides data to support our analysis, we used coverage-based rarefaction and extrapolation curves for each elevational stage (upland and highland) to compare and estimate species richness among elevational stages with different numbers of individuals collected (Colwell et al. 2012; Chao et al. 2014). The interpolated and extrapolated values for abundance data were based on Hill numbers (q = 0) and were generated in the iNEXT package (Hsieh et al. 2016).

To evaluate the butterfly richness, abundance, and composition along the Uei Tepui elevational gradient, we ran Generalized Linear Models (GLMs). Because the sampling effort was lower in the highest plots, we included an 'offset' term (log-transformed trap-days) in the models to standardize comparisons across plots. The offset acts as a known adjustment factor, allowing the model to account for differences in sampling effort by scaling the expected response without estimating an additional parameter (Crawley 2013). We used the number of species and the number of individuals as the dependent variables, with elevation as the predictor. We selected a quasi-Poisson distribution for both models due to overdispersion (Zuur et al. 2009). For community composition, we first reduced the dimensionality using Non-metric Multidimensional Scaling (NMDS) based on Bray-Curtis dissimilarities. The species-abundance data were standardized by the total abundance of butterflies per plot to make the ordination more sensitive to the composition rather than the total abundance. We performed a GLM using the one-dimensional NMDS solution as the dependent variable and altitude as an explanatory variable. For this analysis, we used the Gaussian error distribution (Crawley 2013). To better illustrate the species composition variation along the elevational gradient, we plot the relative species abundances along the elevation gradient (Dambros 2020; for the total species sampled, see Supplementary Material, Figure S2). We used "metaMDS" and "vegdist" functions from the package "vegan" (Oksanen et al. 2019) to calculate the NMDS axis.

We compared the Sørensen dissimilarities of butterflies' composition between the elevational stages of upland and highlands. We defined the highlands where Pantepui endemic species started to occur regularly, with all plots above presenting endemic species, since the beginning of the highlands depend on the *tepui* environment and the focal organism (Huber 1987; Rull et al. 2019a). We used abundance data from standardized sampling plots to estimate which β-diversity component (turnover or nestedness) dominated in each elevational stage. To assess the spatial β-diversity, we obtained a multisite dissimilarity value for each component in the upland and highland butterfly communities using the "beta_div" function (see Legendre 2014). To assess whether multisite β-diversity differs among the elevational stages, we calculated bootstrap 95% confidence intervals. We identified significant differences in the lack of overlap between 95% confidence intervals (Manly 2007). All bootstrap analyses were based on 999 randomizations using half of the samples in each permutation.

We conducted all analyses using version 4.1.0 of the R program (R Core Team 2021).

RESULTS

We sampled 299 individuals from 93 species of butterflies in the Uei Tepui, 241 individuals of 57 species of fruit-feeding and 58 individuals of 36 species of nectar-feeding butterflies (Table S2). Among those, 89 individuals belonging to 43 species were collected with opportunistic surveys, with 22 species sampled exclusively with this method. These individuals collected with opportunistic surveys were not included in the analysis below.

In the standardized sampling plots, we collected 210 butterflies belonging to 71 species from five families: Nymphalidae (60 spp), Riodinidae (6 spp), Pieridae (2 spp), Lycaenidae (2 spp), and Hesperiidae (1 sp). Only four species had ten or more individuals collected: *Taygetis laches* (Fabricius, 1793) (n = 35), *Nhambikuara furina* (Hewitson, 1862) (n = 14), *Antirrhea ulei* (Strand, 1912) (n = 12), and *Amiga arnaca* (Nakahara, Willmott & Espeland, 2019) (n = 10). Singletons represented 49% and doubletons accounted for 21% of the sampled specimens. However, in the highland, there was a large dominance of *A. ulei*, which corresponded to 52% of the sampled individuals up to 1500 m a.s.l. The sampling completeness suggests that our sampling effort recorded ~84% of species in the uplands and ~73% of the estimated species richness for the highland (Figure S1).

Butterfly richness (t = -4.146, p = 0.001) and abundance (t = -4.893, p < 0.001) strongly decreased with altitude. There was a marked change in richness and abundance above 1330 m a.s.l. where the average number of species and individuals was nearly half of the lower altitude plots (Figure 2a,b). The one-axis NMDS solution converged and had moderate stress (0.13). Species composition also varied strongly with elevation (GLM; $R^2 = 0.83$, $t = -7.38$, $p < 0.001$; Figure 2c).

Among standardized samples, 74% of the species (n = 53) were recorded at least once in previous studies in the lowlands of the Brazilian Amazon (reference studies in the Table S3). Most of these species (n = 50) were sampled from 1000-1100 m a.s.l. Endemic species were detected in all sampling plots above 1330 m a.s.l. (Figure 3). The first endemic species of Pantepui caught in the sampling plots was the new subspecies *Caligo suzanna weidmanni* (Blandin, Attal, Orellana, Nield, Lamas & Costa, 2025) (Costa et al. 2025) at the 1330 m elevation. Of the 13 species sampled in the plots above this elevation, six (46%) were endemic to Pantepui, with *A. ulei* being the most frequent species from 1390 m to 1820 m a.s.l. (Figure 3). The endemism rate increases to 55.5% (10 of 18 species; Figure 4) when considering individuals sampled in opportunistic sampling events above 1330 m a.s.l. (not included in the main analysis).

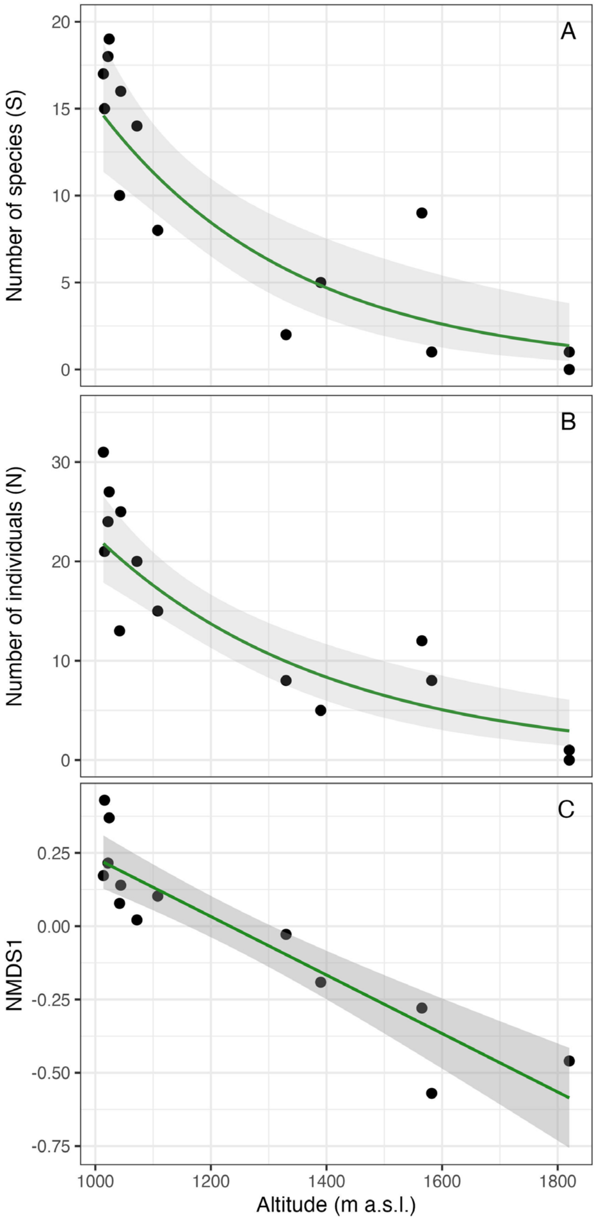

Figure 2. Linear regression of the effect of elevation on **(A)** number of species, **(B)** number of individuals, and **(C)** butterfly composition along the altitudinal gradient of Uei Tepui, Roraima State, Brazil. Points represent each sampling plot, and the shaded areas represent 95% of the confidence intervals.

Species turnover accounted for 89% of the observed compositional variation among our sampling plots across the elevational gradient. Although the total β-diversity (species dissimilarity) was higher in the highland plots than in the upland plots, this difference was not statistically significant (Figure 5a). Interestingly, despite the relatively small difference in altitude between the upland sampling plots, the spatial turnover was significantly greater in the upland butterfly communities (93%) compared to the highland communities (69%) (Figure 5b).

DISCUSSION

For the first time, we were able to study and describe the butterfly assemblage structure across a continuous elevation gradient in this isolated *tepui*. We found that despite the unique environmental aspects of the Brazilian side of the Uei Tepui, the butterfly community followed the general patterns of community structure observed along elevational gradients in the Pantepui mountains. We found a marked change in species richness, abundance, and composition around 1330 m. Above this point, we also found lower species replacement and higher occurrence of endemic species.

Butterfly richness and abundance have been shown to decrease with altitude in most of the studies along altitudinal gradients of Brazilian mountain chains (Espinhaço [Beirão et al. 2020; Pires et al. 2020], Serra da Mantiqueira [Henriques et al. 2022], and Serra do Mar [Carneiro et al. 2014]). This is a typical pattern found for butterflies and other organisms around the world (Acharya and Vijayan 2015; Perillo et al. 2017; Castro et al. 2019; Berrones-Morales et al. 2020; Afzal et al. 2021; Dzekashu et al. 2022). Specifically in the Guiana Highlands, several taxa present a similar pattern, including plants (Berry and Riina 2005), other invertebrates (Ochoa and Rojas-Runjaic 2019; Nogueira et al. 2021) and mammals (Lew and Lim 2019).

There are some general explanations for the decline in species richness and abundance with increasing elevation. Area reduction toward the summit is a notable limiting factor for species diversity (Rahbek 1997; Safont et al. 2014; Ochoa and Rojas-Runjaic 2019; Riina et al. 2019). This area effect is likely to be particularly relevant in the Uei Tepui, which has one of

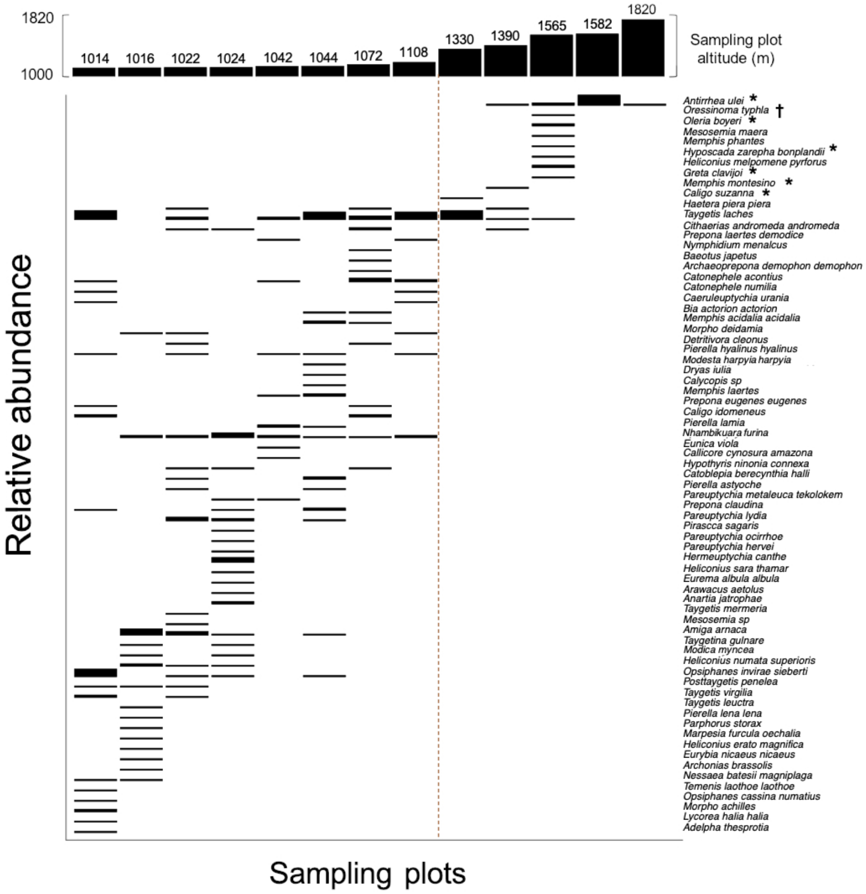

Figure 3. Direct ordination of butterfly species and their relative abundance (bar thickness) with the elevational gradient in Uei-tepui, Roraima State, Brazil. * butterflies endemic to Pantepui; † new species record to Brazil. The dashed line represents the lowest altitude where the first endemic species was collected in the sampling plots.

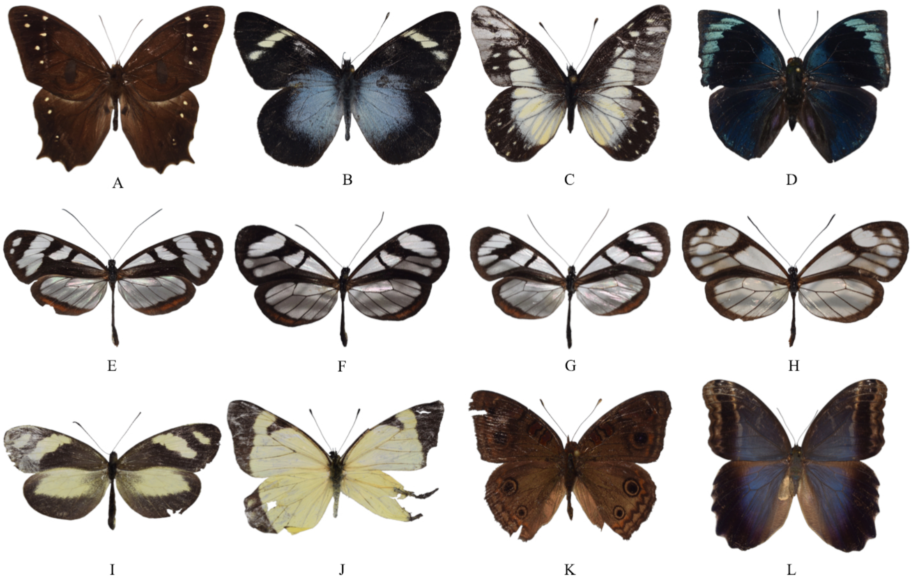

Figure 4. Endemic butterflies from Pantepui sampled in Uei Tepui, Roraima state, Brazil. **(A)** *Antirrhea ulei*; **(B)** *Pereute lindemannae pemona**; (**C**) *Archonias sisamnus ayanganna**; **(D)** *Memphis montesino*; **(E)** *Hyposcada zarepha bonplandii*; **(F)** *Oleria boyeri*; **(G)** new species of *Oleria sp.**; **(H)** *Greta clavijoi*; **(I)** *Dismorphia zathoe proserpina**; **(J)** *Melete leucardia reyi***; **(K)** *Junonia evarete oscura***; **(L)** *Caligo suzanna weidmanni.* * = sampled opportunistically; ** sampled opportunistically in an open field in the upland.

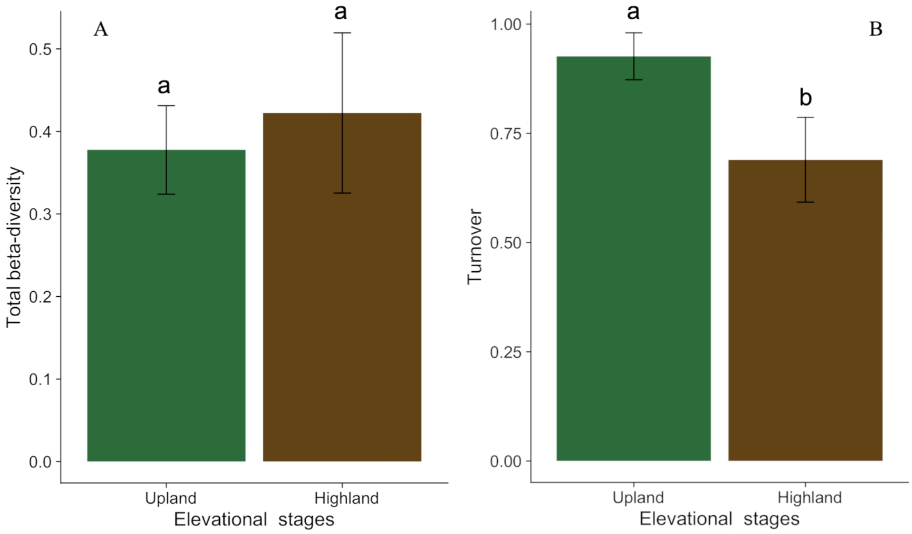

Figure 5. The relative contribution of **(A)** total β-diversity and **(B)** spatial turnover among the elevational stages. The bars represent the observed multisite component values, and the black lines represent 95% confidence intervals based on 999 bootstraps. Different letters indicate significant differences between upland and highland butterfly communities based on the lack of confidence interval overlap.

the smallest summits and slope areas among *tepuis* (Rull et al. 2019a). Spatial limitation tends to select more specialized biota, decreasing diversity and increasing endemism (Viloria and Costa 2019). This pattern was described for plant communities in different *tepuis* in the Guiana Highlands (Berry and Riina 2005), and this compositional change may also influence the butterfly community.

The presence of host plants and life strategies strongly influences the distribution of butterflies, with larval specificity and habitat specialization being critical determinants of species occurrence (Dennis et al. 2004; Koh et al. 2004; Hodkinson 2005). Consequently, the strong compositional dissimilarity of butterflies along the elevational gradient reported here may also result from the phytogeographical changes along the *tepuis* (Viloria and Costa 2019).

Besides the spatial limitation, higher elevations act as a strong environmental filter on butterflies (Nogué et al. 2012; Chazot et al. 2014; Henriques et al. 2022). Climatic conditions, especially temperature, greatly influence ectothermic organisms, acting not only in the time of their activity during the day but also in growth, development, and seasonality (Hodkinson 2005). During our study, the rainfall was prevalent, especially in the highlands, where the temperature was much cooler than in the uplands. This likely explains the low number of butterfly individuals sampled during the expedition compared to other mountainous regions in the Neotropics (Marín et al. 2015; Henriques et al. 2019; Álvarez et al. 2021). However, because there are no studies in the Pantepui that include the number of species and abundance data, and the majority of butterfly studies in *tepuis* focus on species descriptions or the occurrence of new species in certain *tepui* (Nakahara et al. 2014; Costa et al. 2014a; Fratello et al. 2015; Costa et al. 2019), we cannot state that our observed abundance was lower than expected by our sampling effort. The absence of species commonly found in Neotropical montane environments, such as the Pronophilina subtribe, might be due to these climatic and seasonal variables. While these butterflies are present mainly in the Andes (Pyrcz et al. 2009; Pyrcz and Rodríguez 2007; Pyrcz et al. 2016), they are also found in some *tepuis*, including the adjacent Roraima massif (Pyrcz and Fratello 2005).

Although we are not able to verify whether the 200 m distance between plots interfered with sampling independence in the highest plots (i.e., 1820 m a.s.l.), the lack of butterflies (we sampled only one individual in the traps and none were observed during active sampling) suggests that this effect was minimal. This minimum distance between sampling plots has been considered adequate to maintain independence between sampling units in the Atlantic Forest (see Ribeiro et al. 2012; Freitas et al. 2014), although such information is lacking for mountainous and Amazonian systems. However, most butterfly individuals move short distances and tend to remain within the same habitat type (Lourenço et al. 2021). In addition, oxygen availability decreases at higher altitudes, which can affect the ability to sustain flight performance in insects (Hodkinson 2005). Because habitat types and abiotic conditions can shift abruptly over short spatial scales along altitudinal gradients (Körner 2007), butterflies at higher elevations are expected to have narrower home ranges. Therefore, this spatial proximity between sampling units is unlikely to have affected our results.

Due to the lower abundance of butterflies observed this study, it is suggested that future studies use both rotten fish and fermented fruit as bait to increase the sampling effectiveness in high altitudinal sites (Álvarez et al. 2021). We did not include those items because our sampling was part of the Brazilian Biodiversity Monitoring Program (Brasil 2022), therefore it was important to maintain the standardized protocol for bait and the number of traps used across other Protected Areas (Nobre et al. 2014).

In this study, butterfly composition changed gradually across the sampling plots along the elevational gradient of the Uei Tepui, but around 1330 m a.s.l., endemic species from Pantepui started to appear regularly. From this altitude, the butterfly richness and abundance decreased dramatically compared to the sampling plots in the 1000-1100 m a.s.l. Despite the general definition of highlands as being above 1500 m a.s.l. (Rull et al. 2019a), our butterfly occurrence data show that the highlands in the Uei Tepui begin around 1330 m. This result is in line with Pantepui characterization, which suggest a significant faunal change and the appearance of endemic species at around 1200-1500 m (Huber 1987). The butterfly endemism rate in the highlands (46%) aligns with the rate of plant species exclusively distributed in the highlands of Pantepui (Berry and Riina 2005; Riina et al. 2019), providing compelling evidence for the cohesive interaction between butterflies and plant composition.

The β-diversity values were similar between the upland and the highland communities. The species replacement (turnover) was the main driver of the differences in composition among our sampling plots along the elevation gradient. This pattern is commonly found in studies of elevational gradients (Beirão et al. 2020; Pires et al. 2020; Cómbita et al. 2022; Montañez-Reyna et al. 2023). As we expected, the species turnover presents a higher contribution in the upland than in the highland communities. Some studies show that species diversity and turnover rates tend to decrease at higher elevations due to stronger environmental filtering and reduced environmental heterogeneity (Beirão et al. 2020; Castro et al. 2020). Our findings underscore the significant decline in species richness at the highest elevation sampled (1820 m a.s.l.), which is crucial in reducing turnover and increasing nestedness.

Although Pantepui is one of the most singular provinces for Neotropical biodiversity and endemism (Rull and Vegas-Villarúbia 2017), its remoteness and difficult access have limited our understanding of its diversity (Costa et al. 2014b; Carvalho et al. 2023). Sporadic expeditions, which began in the mid-19th century and continue to this day, have provided valuable insights into the origin and diversity of organisms in this unique environment (Rull 2019; Rabelo et al. 2021). However, long-term monitoring of both fauna and flora is essential to understand the environmental influences on communities' structure and contribute to conservation strategies (Freitas et al. 2024). This is especially important in the context of climate change which is considered one of the greatest threats to mountain biota worldwide (Forister et al. 2010; Rull and Vegas-Villarúbia 2017; Rull et al. 2019b; Rödder et al. 2021; Chowdhury 2023). Therefore, initiatives like the Brazilian Biodiversity Monitoring Program (*Programa Monitora,* Brasil 2022) and Protected Areas of Amazonia (ARPA) programs (arpa.mma.gov.br) are crucial for advancing this understanding.

CONCLUSION

Our study was the first to evaluate the butterfly assemblage structure along a *tepui* altitudinal gradient using standardized and combined sampling methods. Our results indicate that the Uei Tepui harbors a structured butterfly community shaped by elevation, with reduced richness and abundance at higher altitudes and a distinct shift in composition around 1330 m a.s.l., including a higher occurrence of endemic species. These findings support broader biogeographical patterns observed in other *tepuis* and taxa, reinforcing the role of elevation, spatial limitation, and environmental filtering in shaping Neotropical montane diversity. The distinctiveness of the Pantepui region, combined with its high rates of endemism and vulnerability to climate change, highlights the urgency of expanding research and conservation efforts in these isolated mountain systems.

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SUPPLEMENTARY MATERIAL

Oliveira *et al*. Butterfly (Insecta: Lepidoptera) assemblage structure along an upland-highland elevational gradient in a Brazilian tepui

Table S1. The mean altitude of each sampling plot.

Transect	Plot	Altitude (m a.s.l.)
SS1	P1	1044
SS1	P2	1042
SS1	P3	1072
SS1	P4	1108
SS2	P1	1014
SS2	P2	1022
SS2	P3	1016
SS2	P4	1024
SS3	P1	1330
SS3	P2	1390
SS3	P3	1565
SS3	P4	1582
SS4	P1	1820
SS4	P2	1820

Table S2. The complete list of butterfly species and respective abundances sampled in the first biological expedition to the Brazilian side of Uei Tepui, and the distinct sampling methods used: standardized methods [understory (U) and canopy (C) traps (T) in the sampling plots, and transect walk (TW) using entomological net], and opportunistically surveys (OS, t = traps out of the plots, and N = entomological net).

Family/Subfamily/Species	Altitude (m a.s.l.)	Methods	N° of individuals
Hesperiidae			**2**
Hesperiinae			**1**
Parphorus storax (Mabille, 1891)	1019	TW	1
Pyrginae			**1**
Hyalothyrus infernalis (Möschler, 1877)	956	OS (N)	1
Lycaenidae			**3**
Theclinae			**3**
Arawacus aetolus (Sulzer, 1776)	1021	TW	1
Calycopis sp Scudder, 1876	1018	TW	2
Nymphalidae			**279**
Biblidinae			**24**
Callicore cynosura amazona (H. Bates, 1864)	1041	T (C)	1
Catonephele acontius (Linnaeus, 1771)	from 1015 to 1112	T (U,C), OS (N)	13
Catonephele numilia (Cramer, 1776)	from 1013 to 1109	T (C)	2
Eunica viola Bates, 1864	1043	T (C)	1
Nessaea batesii magniplaga Röber, 1928	from 1015 to 1018	T (U), OS (t)	5
Temenis laothoe laothoe (Cramer, 1777)	from 1014 to 1018	T (C), OS (t)	2
Charaxinae			**27**
Archaeoprepona d. demophon (Linnaeus, 1758)	from 1018 to 1073	T(C), OS (t)	2
Archaeoprepona licomedes (Cramer, 1777)	1018	OS (t)	3
Memphis a. acidalia (Hübner, [1819])	from 1048 to 1063	T (U,C)	3
Memphis laertes (Cramer, 1775)	from 1043 to 1048	T (U,C)	3
*Memphis montesino** Pyrcz, 1995	1388	T (C)	1
Memphis phantes (Hopffer, 1874)	1580	T (C)	1
Mesoprepona pheridamas (Cramer, 1777)	1018	OS (t)	1
Prepona claudina (Godart, [1824])	from 1014 to 1048	T (C)	5
Prepona eugenes eugenes H. Bates, 1865	from 1013 to 1071	T (C), OS (t)	4
Prepona laertes demodice (Godart, [1824])	from 1018 to 1109	T (C), OS (N)	3
Zaretis itys (Cramer, 1777)	1018	OS (N)	1

Table S2. Continued

Family/Subfamily/Species	Altitude (m a.s.l.)	Methods	N° of individuals
Cyrestinae			**1**
Marpesia furcula oechalia (Westwood, 1850)	1019	TW	1
Danainae			**15**
_Greta clavijoi_* Neild, 2008	from 1486 to 1571	TW, OS (N)	3
_Hyposcada zarepha bonplandii_* Neild, 2008	from 1571 to 1581	TW, OS (N)	2
Hypothyris ninonia connexa Hall, 1939	from 1021 to 1071	TW	3
Lycorea halia halia (Hübner, 1816)	1013	TW	1
Melinaea mneme mauensis Weymer, 1891	1018	OS (N)	1
Melinaea satevis crameri Godman & Salvin, 1898	from 920 to 1018	OS (N)	2
_Oleria boyeri_* Neild, 2008	1581	TW	2
Oleria n. sp Hübner, 1816	1571	OS (N)	1
Heliconiinae			**14**
Dryas iulia*** (Fabricius, 1775)	1047	T (C)	1
Heliconius erato magnifica Riffarth, 1900	from 920 to 1019	TW, OS (N)	6
Heliconius melpomene pyrforus Kaye, 1907	1486	TW	2
Heliconius numata superioris Butler, 1875	from 1016 to 1026	TW	4
Heliconius sara thamar (Fabricius, 1793)	1021	TW	1
Limenitidinae			**2**
Adelpha delinita delinita Fruhstorfer, 1913	1018	OS (N)	1
Adelpha thesprotia (C. Felder & R. Felder, 1867)	1014	T (C)	1
Nymphalinae			**9**
Anartia jatrophae*** (Linnaeus, 1763)	1021	TW	2
Baeotus japetus (Staudinger, [1885])	1077	T (C)	1
Colobura dirce (Linnaeus, 1758)	1018	OS (N)	2
_Junonia evarete oscura_* Neild, 2008	920	OS (N)	1
Junonia genoveva vivida W.T.M. Forbes, [1929]	920	OS (N)	2
Siproeta stelenes meridionalis (Fruhstorfer, 1909)	1018	OS (N)	1
Satyrinae			**187**
Amiga arnaca (Fabricius, 1776)	from 956 to 1037	T (U), TW OS (N)	11
_Antirrhea ulei_* Strand, 1912	from 1388 to 1820	T (U,C), TW, OS (N)	14
Bia actorion actorion (Linnaeus, 1763)	from 956 to 1056	TW, OS (t,N)	4
Caeruleuptychia urania (A. Butler, 1867)	from 1013 to 1106	T (U)	2
Caligo idomeneus (Linnaeus, 1758)	from 1016 to 1063	T (U)	5
Caligo illioneus illioneus (Cramer, 1775)	920	OS (N)	1
_Caligo suzanna weidmanni_* Blandin, Attal, Orellana, Lamas & Costa, 2025	from 1018 to 1571	T (C), OS (t,N),	3
Catoblepia berecynthia halli Bristow, 1981	from 1022 to 1047	T (U,C)	3
Catoblepia xanthus (Linnaeus, 1758)	1109	OS (t)	1
Cithaerias andromeda andromeda (Fabricius, 1775)	from 1021 to 1392	TW	5
Emeryus argulus magnum Zacca, Casagrande & Mielke, 2020	920	OS (N)	1
Eryphanis automedon automedon (Cramer, 1775)	1047	OS (t)	1
Haetera piera piera (Linnaeus, 1758)	from 1017 to 1392	TW	3
Hermeuptychia canthe [Hübner, 1811]	from 920 to 1026	TW, OS (N)	7
Manataria maculata maculata (Hopffer, 1874)	1571	OS (N)	1
Modesta h. harpyia (C. Felder & R. Felder, 1867)	1037	T (C)	1
Modica myncea (Cramer, 1780)	1019	T (U), TW	2
Morpho achilles (Linnaeus, 1758)	from 1013 to 1015	T (U), OS (t,N)	3
Morpho deidamia (Hübner, [1819])	from 1016 to 1106	T (U), OS (t,N)	9
Morpho helenor extremus Le Moult, 1933	927	OS (N)	1
Nhambikuara furina (Hewitson, 1862)	from 1019 to 1109	T (U,C), TW, OS (N)	16
Opsiphanes cassina numatius Fruhstorfer, 1912	1014	T (C)	1
Opsiphanes invirae sieberti Bristow, 1991	from 1013 to 1048	T (C)	9
Oressinoma typhla** E. Doubleday, [1849]	from 1538 to 1571	TW, OS (N)	2

Table S2. Continued

Family/Subfamily/Species	Altitude (m a.s.l.)	Methods	N° of individuals
Pareuptychia ocirrhoe (Fabricius, 1776)	1021	TW	1
Pareuptychia hervei Brévignon, 2005	1019	T (U)	1
Pareuptychia lydia (Cramer, 1777)	from 1022 to 1048	T (C), TW	6
Pareuptychia metaleuca tekolokem Brévignon, 2005	from 1019 to 1041	T (U,C)	2
Pierella astyoche (Erichson, [1849])	from 1017 to 1045	TW	2
Pierella hyalinus hyalinus (Gmelin, [1790])	from 1014 to 1090	T (U), TW	5
Pierella lamia (Sulzer, 1776)	from 1039 to 1042	TW	3
Pierella lena lena (Linnaeus, 1767)	1019	TW	1
Posttaygetis penelea (Cramer, 1777)	from 1014 to 1017	T (U), TW	3
Taygetina gulnare (A. Butler, 1870)	1019	TW	2
Taygetis laches (Fabricius, 1793)	from 1013 to 1538	T (U), TW, OS (N)	48
Taygetis leuctra A. Butler, 1870	1017	T (U)	1
Taygetis mermeria (Cramer, 1776)	1022	T (U)	1
Taygetis virgilia (Cramer, 1776)	from 1014 to 1037	T (U), OS (t)	5
Pieridae			**7**
Coliadinae			**1**
*Eurema albula albula**** (Cramer, 1775)	1021	TW	1
Dismorphinae			**1**
Dismorphia zathoe proserpina * Grose-Smith & W.F.Kirby, 1897	1571	OS (N)	1
Pierinae			**5**
Archonias brassolis (Fabricius, 1776)	1019	TW	1
*Archonias sisamnus ayanganna** Bollino & Costa, 2007	1571	OS (N)	1
*Melete leucardia reyi** A.F.E. Neild & Costa, 2017	927	OS (N)	1
*Pereute lindemannae pemona** de Marmels, Clavijo & M. Chacín, 2003	1571	OS (N)	2
Riodinidae			**8**
Riodininae			**8**
Detritivora cleonus (Stoll, 1781)	from 1017 to 1071	TW	2
Eurybia nicaeus nicaeus (Fabricius, 1775)	1016	TW	1
Mesosemia maera Hewitson, 1873	1486	TW	1
Mesosemia sp. Hübner, [1819]	1017	TW	1
Nymphidium menalcus (Stoll, 1782)	from 1018 to 1071	TW, OS (N)	2
Pirascca sagaris (Cramer, 1775)	1021	TW	1
Total			299

* Endemic to the Pantepui (Viloria and Costa 2019; Costa et al. 2025). With the opportunistic sampling, we were also able to record endemic species outside the sampling plots. Some of these were found below 1330 m a.s.l.; however, this is consistent with studies on butterflies from the Pantepui region, where the butterfly endemism appears gradually from ~1000 m a.s.l. and increases up to 1500 m (Viloria and Costa 2019).
** First record in Brazil, but it is distributed from Costa Rica to Ecuador, Colombia, Venezuela, and Bolivia (Losada et al. 2018; pers. comm.).
*** Common butterfly species in open areas and not usually sampled in the forest.

Table S3. Butterfly species recorded in the sampling plots of this study, and the butterfly records in different studies across the Brazilian Amazon lowlands. x = recorded species; x sp = same species recorded but not the same subspecies.

This study	Emmel and Austin (1990)	Ramos (2000)	Barlow et al. (2007)	Mielke et al. (2010)	Casagrande et al. (2012)	Ribeiro and Freitas (2012)	Graça et al. (2017a)	Graça et al. (2017b)	Teston and Silva (2017)	Spaniol et al. (2019)	Oliveira et al. (2021)	Rabelo et al. (2021)	Mota et al. (2022)
A. thesprotia	x												x
A. arnaca	x	x							x	x	x		x
*A. jatrophae****				x									
*A. ulei**													
A. aetolus					x								
A. d. demophon	x	x	x	x	x	x	x		x	x	x	x	x
A. brassolis													
B. japetus			x			x				x			x
B. a. actorion	x	x	x	x	x	x	x	x	x	x	x	x	

Table S3. Continued

This study	Emmel and Austin (1990)	Ramos (2000)	Barlow et al. (2007)	Mielke et al. (2010)	Casagrande et al. (2012)	Ribeiro and Freitas (2012)	Graça et al. (2017a)	Graça et al. (2017b)	Teston and Silva (2017)	Spaniol et al. (2019)	Oliveira et al. (2021)	Rabelo et al. (2021)	Mota et al. (2022)
C. urania													
C. idomeneus	x		x	x				x	x	x			x
*C. suzanna weidmanni**			x sp										
C. c. amazona	x sp		x sp										x sp
Calycopis sp													
C. b. halli	x sp	x sp	x sp	x sp	x sp	x sp			x sp	x sp	x sp	x sp	x sp
C. acontius	x	x			x	x	x	x	x	x	x	x	x
C. numilia		x				x					x		x
C. a. andromeda			x		x			x		x			
D. cleonus	x			x	x								
*D. iulia****	x			x sp	x						x		
E. viola													
*E. a. albula****	x			x							x		x
E. n. nicaeus	x			x	x						x		x
*G. clavijoi**													
H. p. piera	x			x sp	x			x	x	x	x	x	x
H. e. magnifica	x sp			x sp	x sp						x sp	x sp	x sp
H. m. pyrforus	x sp			x sp	x sp								
H. n. superiores	x sp			x sp	x						x sp		x
H. s. thamar	x sp		x sp	x							x sp	x sp	x sp
H. canthe													
*H. z. bonplandii**													
H. n. connexa	x sp												x sp
L. h. halia				x sp									x sp
M. myncea	x		x			x		x			x		x
M. h. harpyia			x		x sp			x			x sp		x sp
M. f. oechalia													
M. a. acidalia			x	x sp		x	x		x	x			x
M. laertes			x			x	x	x					
*M. montesino**													
M. phantes			x	x		x		x		x	x sp		
M. maera													
Mesosemia sp													
M. achilles	x	x sp	x	x sp	x				x		x	x	x sp
M. deidamia	x		x		x				x			x	x
N. b. magniplaga													
N. furina			x		x								
N. menalcus													
*O. boyeri**													
O. c. numatius			x sp										
O. i. sieberti	x sp	x sp	x sp	x sp		x sp	x sp	x sp		x sp	x sp	x sp	x sp
*O. typhla***													
P. ocirrhoe		x							x			x	x
P. hervei													
P. lydia			x			x				x			x
P. m. tekolokem		x sp											
P. storax	x			x									
P. astyoche	x			x sp	x			x		x	x		x sp

Table S3. Continued

This study	Emmel and Austin (1990)	Ramos (2000)	Barlow et al. (2007)	Mielke et al. (2010)	Casagrande et al. (2012)	Ribeiro and Freitas (2012)	Graça et al. (2017a)	Graça et al. (2017b)	Teston and Silva (2017)	Spaniol et al. (2019)	Oliveira et al. (2021)	Rabelo et al. (2021)	Mota et al. (2022)
P. h. hyalinus	x		x		x			x					x
P. lamia	x				x			x		x			
P. l. lena	x			x	x		x			x	x sp	x	x
P. sagaris													
P. penelea	x		x	x			x				x	x	x
P. claudina	x		x	x sp		x	x	x	x				x
P. e. eugenes													x
P. l. demodice		x sp	x	x	x sp					x			x sp
T. gulnare													x
T. laches		x	x		x	x	x	x	x	x	x		x
T. leuctra		x	x										
T. mermeria	x	x	x						x		x	x	x
T. virgilia	x	x	x		x				x		x	x	x
T. l. laothoe	x		x	x		x	x		x	x	x	x	x

* Endemic from Pantepui (Viloria and Costa 2019; Costa et al. 2025)
** First record in Brazil, but it is distributed from Costa Rica to Ecuador, Colombia, Venezuela, and Bolivia (Losada et al. 2018; pers. comm.).
*** Common butterfly species in open areas and not usually sampled in the forest.
Butterfly studies in the Brazilian Amazonia lowlands: Emmel and Austin (1990) in Rondônia State; Barlow et al. (2007) in Amapá and Pará States; Graça et al. (2017a) in Roraima State; Casagrande et al. (2012), Ribeiro and Freitas (2012), Graça et al. (2017b), Spaniol et al. (2019), Oliveira et al. (2021), and Rabelo et al. (2021) in Amazonas State, and Mota et al. (2022) in Mato Grosso State.

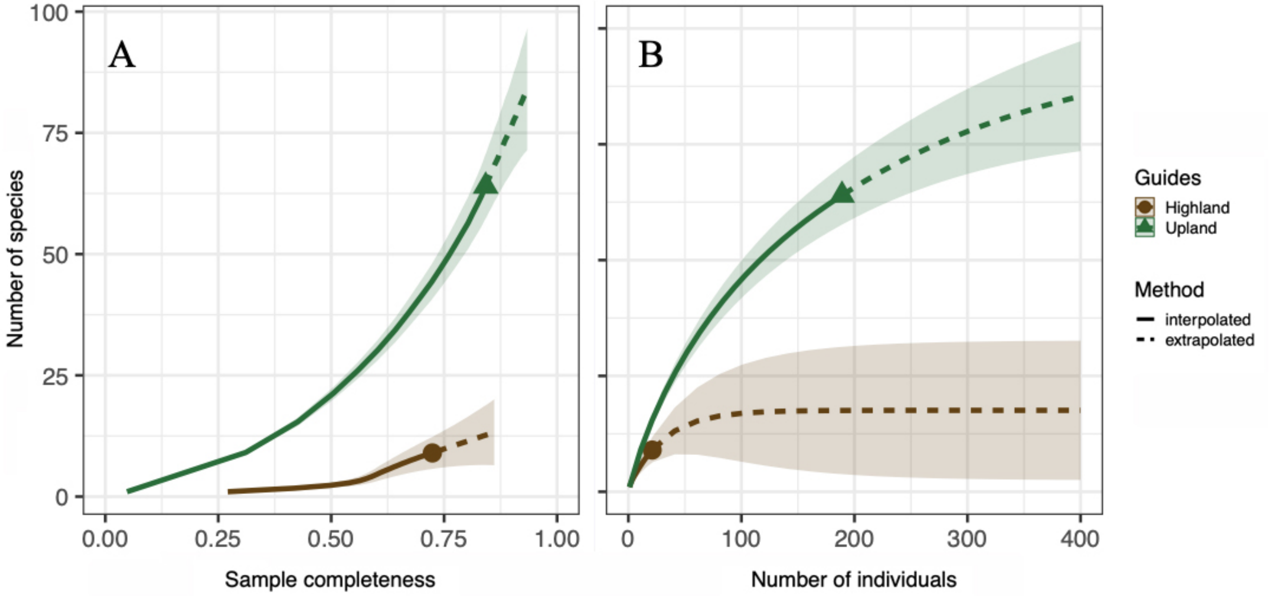

Figure S1. **(A)** Sample completeness and **(B)** individual-based rarefaction curves for upland and highland elevations (triangles and circles, respectively) of butterfly assemblages in the Uei Tepui, Roraima State. Solid lines represent the interpolated and dashed lines the extrapolates values. Shaded areas represent 95% confidence intervals.

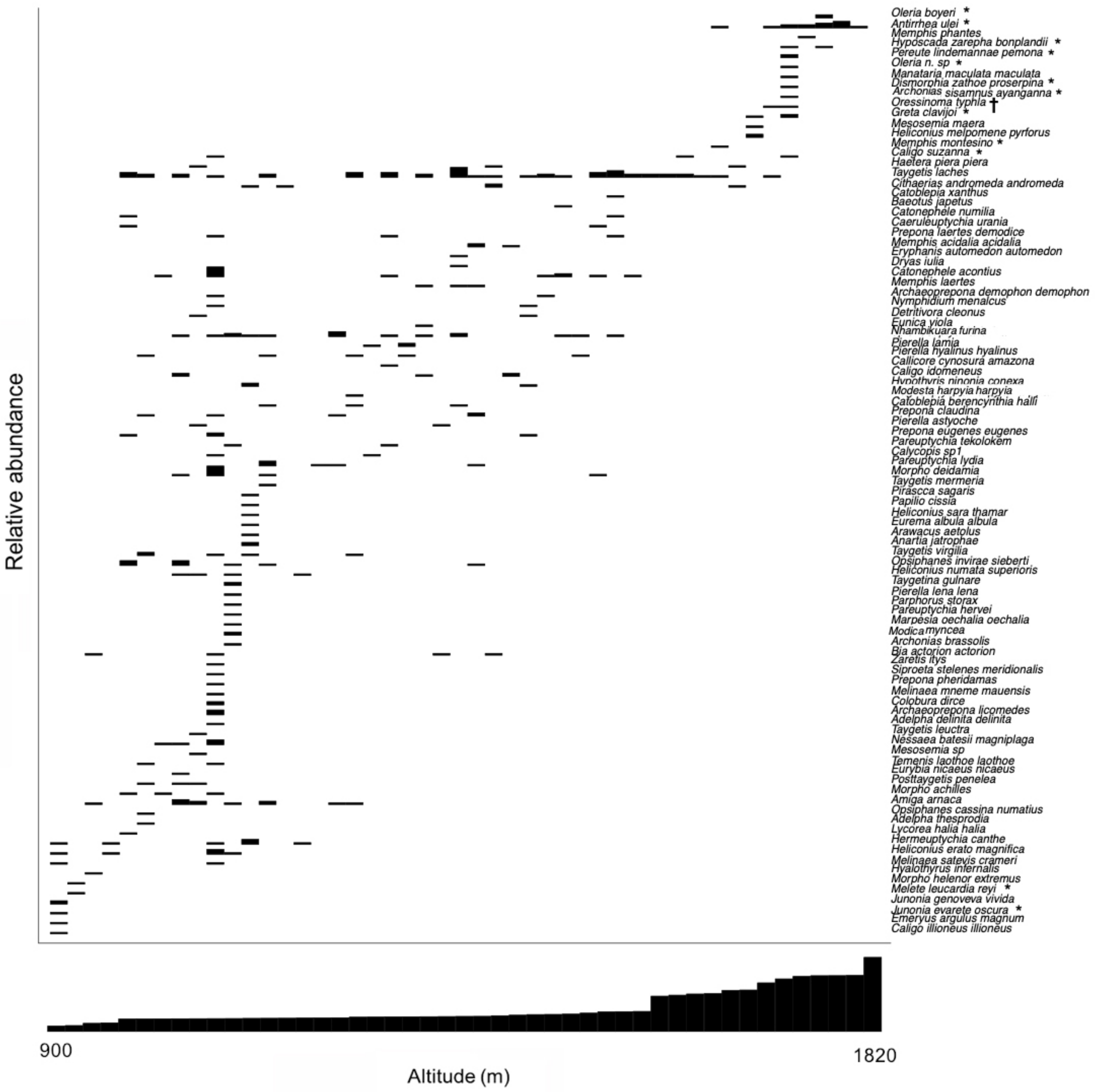

Figure S2. Direct ordination of all butterfly species sampled in this study (standardized and opportunistically sampled) and their relative abundance (bar thickness) along the elevational gradient of the Uei-tepui, Roraima State, Brazil. * butterflies endemic to Pantepui; **†** new species record to Brazil.

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